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RESEARCH ARTICLE

The metabolic cost of *in vivo* constant muscle force production at zero net mechanical work

Tim J. van der Zee‡,*, Koen K. Lemaire and Arthur J. van Soest

ABSTRACT

The metabolic cost per unit force is generally thought to increase with the mechanical work done by the muscle fibres. It is currently unclear how the metabolic cost of doing alternating positive and negative muscle fibre mechanical work relates to the metabolic cost of doing zero muscle fibre mechanical work at similar muscle force. The current study aimed to investigate this issue by comparing *in vivo* metabolic power between a dynamic and an isometric near-constant force production task. In both tasks, participants performed periodic movement about the knee joint in the gravitational field. Therefore, net external mechanical work was constrained to be zero. The tasks mainly differed from each other in average positive knee joint mechanical power, which was 4.3±0.5 W per leg during the dynamic task and 0.1±0.1 W per leg during the isometric task. Knee extension torque was near-constant around 15.2±1.7 N m during the dynamic task and around 15.7±1.7 N m during the isometric task. Owing to near-constant knee extension torque, quadriceps tendon length was presumably nearly constant during both tasks. Therefore, knee joint mechanical work was predominantly done by the muscle fibres in both tasks. Average gross metabolic power was 3.22±0.46 W kg^{-1} during the dynamic task and 2.13±0.36 W kg^{-1} during the isometric task. Because tasks differed mainly in the amount of positive muscle fibre mechanical work, these results imply that the metabolic cost of near-constant force production *in vivo* at zero net mechanical work can be reduced by minimizing positive muscle fibre mechanical work.

KEY WORDS: Energetics of periodic movement, Metabolic cost of force production, Quadriceps contraction, Single-joint movement, Muscle fibre mechanical work

INTRODUCTION

Animal movement is accomplished through forces acting from muscle–tendon complexes on bony structures, giving rise to rotational movement in joints. During these rotations, muscle–tendon complexes change length while delivering force and thus do positive and/or negative mechanical work. Positive muscle–tendon complex mechanical work, however, does not necessarily imply positive muscle fibre mechanical work. For example, during human walking and running, the Achilles tendon fibres take up a large part of the change in triceps surae muscle–tendon complex length (Lichtwark and Wilson, 2006); as a result, the muscle fibres contract near-isometrically and hence do near-zero positive mechanical work.

During periodic movement, metabolic energy consumption within the muscle fibres constitutes a considerable part of the total metabolic energy consumption (i.e. the 'metabolic cost'). Apart from consuming metabolic energy when doing mechanical work, muscle fibres consume metabolic energy when delivering force during isometric contraction (Ryschon et al., 1997; Beltman et al., 2004; Ortega et al., 2015). Maximally activated muscle fibres *in vitro* consume substantially more metabolic energy per unit force when shortening (doing positive mechanical work) compared with when contracting isometrically (doing no positive mechanical work) (Fenn, 1924; Hill, 1938). Submaximally activated muscle fibres *in vivo* require about 3.6 times more metabolic energy per unit force when shortening and doing positive mechanical work, compared with when lengthening and doing negative mechanical work (Abbott et al., 1952). For both maximally activated muscle fibres *in vitro* (Beltman et al., 2004) and submaximally activated muscle fibres *in vivo* (Ortega et al., 2015; Ryschon et al., 1997), there is little or no difference between the metabolic cost per unit force when contracting isometrically and the metabolic cost per unit force when doing negative mechanical work. During many *in vivo* periodic movements, muscle–tendon complexes do alternating positive and negative mechanical work. Taken together, previous observations on the metabolic cost of muscle fibre contractions (i.e. Fenn, 1924; Hill, 1938; Abbott et al., 1952; Ryschon et al., 1997; Beltman et al., 2004; Ortega et al., 2015) lead to the expectation that alternating positive and negative mechanical work requires more metabolic energy than isometric muscle fibre contraction at similar muscle force and similar net mechanical work. However, to our knowledge, for submaximally activated muscle fibres *in vivo*, metabolic cost has not been compared between isometric contractions and contractions that involve alternating positive and negative mechanical work, at equivalent net mechanical work and similar muscle force.

In the current study, *in vivo* whole-body metabolic power was assessed during two different single-joint knee movement tasks in which knee joint torque was delivered at a near-constant level, such that muscle was continuously activated. During one of the two tasks, joint angle was constant, such that positive and negative muscle fibre mechanical work were negligible. During the other task, joint angle fluctuated substantially, such that periods of substantial positive and negative muscle fibre mechanical work production alternated. Net mechanical work was negligible in both tasks and the constant-level torque had a similar value in both tasks.

MATERIALS AND METHODS

Outline of the study

Participants performed both an isometric and a dynamic task that required delivering knee extension torque while seated in a chair. Bilateral, in-phase, 1 degree of freedom (DOF) lower leg movement about the knee joint was the only movement allowed. During both

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tasks, a lead strap weighing 2 kg was attached around each ankle. Kinetic and kinematic variables were calculated from motion capture data, and metabolic power was estimated using respirometry. Participants were provided with real-time feedback on their lower leg angle and were requested to track a predefined target motion, which was constructed such that the knee extension torque was constant and of similar value for both tasks. Surface electromyography (EMG) of the antagonistic muscles operating around the knee was recorded to quantify the extent to which co-contraction occurred.

Participant characteristics

Inclusion criteria were being adult, young (<40 years old) and physically fit; these criteria were pre-established. Sixteen participants (3 females) were recruited for the current study. Age, body length and body mass of participants were 24.0±3.7 years, 180±7 cm and 70.2±9.3 kg (means±s.d.), respectively. Shank and foot inertial properties were measured according to the definitions from Zatsiorsky (2002, p. 599). Foot and shank circumference were 24.4±1.7 cm and 36.4±2.5 cm, respectively; foot and shank length were 26.1±1.4 cm and 40.2±2.3 cm, respectively. Prior to the experiment, informed consent was obtained from each participant. All methods and procedures were approved by the ethical committee of the Vrije Universiteit Amsterdam and were in accordance with Dutch law.

Set-up

An overview of the experimental set-up is shown in Fig. 1A. During the experiment, the participant sat in a chair with both trunk and thighs fixed at a constant angle and lead straps weighing 2 kg attached to each ankle. Lead strap, shank and foot were combined into a single 'lower leg' segment (LL), which was modelled as a rigid body. Using shank, foot and lead strap inertial properties, LL inertial parameters were estimated with respect to the knee. In these estimations, foot centre of mass distance from the knee was assumed to equal shank length. Shank centre of mass distance from the knee was estimated from shank length based on de Leva (1996). The lead strap centre of mass distance from the knee was defined as the distance between the lateral femoral epicondyle and the middle of the lead strap. LL mass, LL moment of inertia with respect to the knee and centre of mass distance from the knee were 6.09±0.58 kg, 0.63±0.11 kg m^2 and 0.29±0.02 m (means±s.d.), respectively. Motion capture measurements were performed to determine LL angle, which was used to calculate the knee torque through inverse dynamics. Optotrak (Northern Digital, Ontario, Canada) active markers were attached on the lateral femoral epicondyle of each leg and on the lateral side of each lower leg just above the lead strap. Optotrak marker locations were sampled at 100 Hz. As indicated in Fig. 1A, for each leg, LL angle was defined as the angle between the line passing through both Optotrak markers attached to that leg and the positive horizontal axis (x-axis) of a right-handed reference frame, originating in the lateral femoral epicondyle marker. The x-axis was orthogonal to the positive vertical axis (y-axis), which was directed opposite to the gravitational force vector (see Fig. 1A). The participant received real-time feedback of both LL angles in the form of a continuous time trace displayed on a monitor in front of the chair, using a custom-made Labview interface (National Instruments Corporation, Austin, TX, USA). Surface EMG recordings were taken to quantify the activation of antagonistic muscles operating around the knee. Bipolar EMG electrodes (Ambu, Ballerup, Denmark) were attached at an inter-electrode distance of 20 mm on the m. gastrocnemius lateralis and the m. biceps femoris of the right leg, at 1/3 of the line between the head of the fibula and the heel and 1/2 of the line between the ischial tuberosity and the lateral epicondyle, respectively (SENIAM guidelines; Hermens et al., 1999). EMG recordings were sampled at 1000 Hz, using a 16-bit Porti 7 data acquisition device (TMS International, Oldenzaal, The Netherlands). EMG was not recorded from the knee extensor muscles. Respirometry measurements were performed to quantify the difference in metabolic cost between tasks. To this end, the rate of oxygen uptake ($\dot{V}_{O_2}$) and the rate of carbon

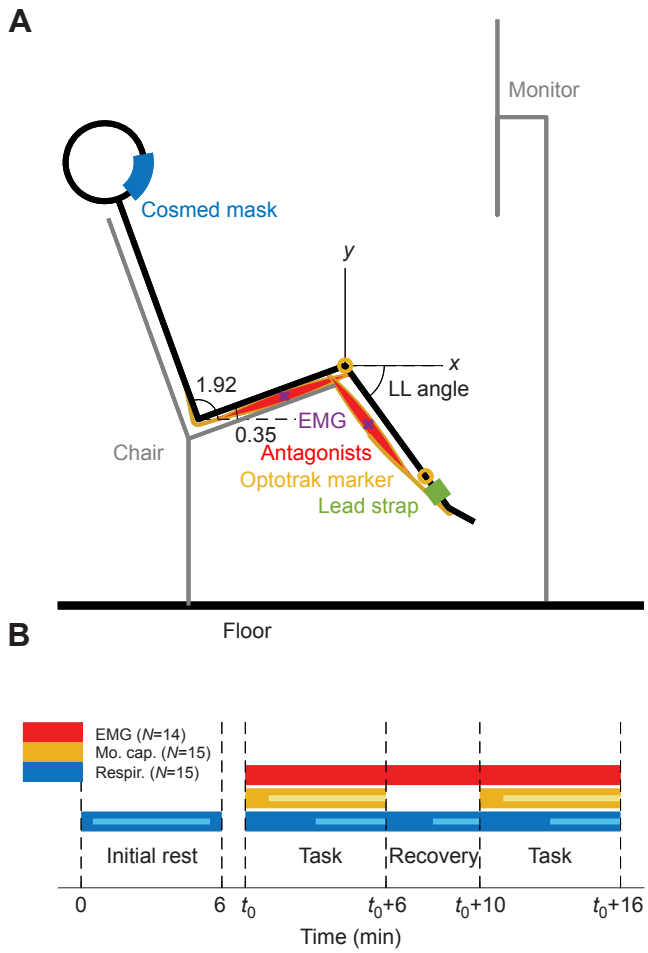

Fig. 1. Experimental set-up and procedures. (A) Experimental set-up. The participant sat in a chair with both trunk and thigh fixed, while wearing 2 kg lead straps around each ankle (green filled rectangle). Both left and right lower leg (LL) angles were displayed in real-time on a monitor in front of the participant, together with two periods of the pre-calculated target angle. Kinematics were recorded using Optotrak markers attached to the lateral epicondyles of both legs, and to the lateral tibia just above each lead strap (yellow open circles). Muscle activation was recorded using electromyography (EMG) electrodes attached to m. gastrocnemius lateralis and m. biceps femoris of the right leg (purple crosses). Respirometry measurements were taken using a Cosmed respirometry measurement device. LL angle was defined with respect to the positive horizontal axis of a right-handed reference frame originating in the lateral epicondyle marker, with its positive vertical axis pointing against the gravitational force vector. Thigh and trunk angle were defined with respect to the positive horizontal axis of a second reference frame originating in the hip and were fixed at 0.35 rad and 1.92 rad, respectively. During the dynamic task, LL angle was varied between −0.17 rad and −0.70 rad. (B) Experimental procedures. Respirometry (Respir.) measurements (N=15) were taken during two 6 min tasks (i.e. dynamic and isometric) and two rest intervals of 6 min (Initial rest) and 4 min (Recovery). For both tasks and the recovery, the second half was used for calculation of mean metabolic power (accentuated). Motion capture (Mo. cap.) measurements (N=15) were taken during both tasks and analysed during the last 5 min of each task (accentuated). EMG measurements (N=14) were taken during both tasks and the recovery.

dioxide production were measured using the K4B2 system (Cosmed, Rome, Italy).

Experimental procedures

An overview of the experimental procedures is shown in Fig. 1B. After measuring the participant's anthropometrics, EMG signals were recorded during maximal voluntary contractions (MVCs) of the ankle plantarflexors and the knee flexors. Next, the participant was seated in the chair and the lead straps were attached around the ankles. Subsequently, the participant was required to practise the dynamic task for 5 min. After the practice trial, the participant had at least 5 min of rest before starting the actual experiment, which consisted of two 6-min tasks (i.e. dynamic and isometric) and two periods of rest (4 min and 6 min, see Fig. 1B). Participants were alternately assigned to either group A or group B. The former group first performed the dynamic task and subsequently the isometric task, whereas the latter group followed the opposite order.

Tasks

Both tasks required the participant to track a target LL angle time-series, with both legs moving in-phase with respect to each other. For both tasks and for each participant separately, construction of the target LL angle time-series was based on the participant's LL inertial properties, the assumption that LL movement was 1-DOF in the aforementioned reference frame, and the assumption that the knee joint axis did not move. For the dynamic task, the target LL angle time-series was constructed such that the knee extension torque had a constant value that resulted in periodic oscillation of LL angle between −0.17 rad and −0.70 rad. Note that a constant knee torque during the dynamic task could be achieved because the current set-up allowed for fluctuations in gravitational torque cancelling out inertial contributions. Given the inertial properties and the predefined desired range of motion, there was only one specific LL angle time-series for which the knee torque was constant (see Appendix); the oscillation frequency ranged from 0.50 to 0.58 Hz between participants. The dynamic task range of motion was chosen based on pilot experiments, in which it was established that participants were well able to comply with the task, while $\dot{V}_{O_2}$ could be easily distinguished from its resting value. We hypothesized that the dynamic task required a greater mean metabolic power than the isometric task. Therefore, we chose the isometric task to require, if anything, a slightly greater average torque than the dynamic task, to prevent the hypothesized difference in mean metabolic power being due to a difference in average torque of the same sign. This was accomplished by choosing each participant's isometric task constant LL angle target such that static equilibrium was achieved with a knee torque that was 0.5 N m greater than the constant knee torque during the dynamic task. For both tasks, net knee joint mechanical work equals the net mechanical work done by the force of gravity. Net knee joint mechanical work was zero because there was no net displacement and thus no net change in potential energy in both tasks.

Data analysis

Planar kinematics were derived from the motion capture data. Kinetics were derived from kinematics using inverse dynamics analysis, under the same assumptions as used to construct the real-time LL angle feedback signal. Motion capture data were analysed using MATLAB (MathWorks, Natick, USA) from 1 min after task initiation up to the end of each task (see Fig. 1B). LL angle data were filtered using a bidirectional second order low-pass Butterworth filter with a 10 Hz cut-off frequency. The average frequency at which fluctuations in knee torque occurred was determined as the frequency at which the power spectral density of the mean-subtracted knee torque time-series was maximal. Power spectral density was calculated with a Welch periodogram technique (Welch, 1967), using six 120 s Hamming windows with 20 s overlap. LL angular velocity and acceleration were obtained by numerically differentiating LL angle with respect to time once and twice, respectively, both using a 5-point differentiator. Instantaneous knee joint mechanical power was calculated as the product of LL angular velocity and knee torque. Net knee joint mechanical work was obtained by numerically integrating the instantaneous knee joint mechanical power with respect to time, using a trapezoid method for the whole 300 s time interval over which motion capture data were analysed. Positive knee joint mechanical work was obtained by numerically integrating the instantaneous knee joint mechanical power with respect to time over the intervals where instantaneous knee joint mechanical power was positive, again using a trapezoid method. Average net and average positive knee joint mechanical power were defined as the net and positive knee joint mechanical work divided by the 300 s time interval over which motion capture data were analysed. $\dot{V}_{O_2}$ was converted to metabolic power (in Watts) according to the relationship between respiratory exchange ratio (RER) and the amount of energy liberated per litre of oxygen consumed (Lusk, 1917). For each of the tasks, metabolic power was averaged over the last 180 s (see Fig. 1B). For the recovery, metabolic power was averaged over the last 120 s. All EMG measurements were bandpass filtered using a bidirectional second order Butterworth filter with cut-off frequencies of 20 Hz and 500 Hz (de Luca, 1997) and a bidirectional fourth order notch filter with cut-off frequencies of 49 Hz and 51 Hz. EMG amplitude was determined as the absolute of the Hilbert transformed signal (Hilbert, 1912), smoothed using a moving average with a width of 0.10 s that moved along every 0.01 s (Burden and Bartlett, 1999). MVCs of m. gastrocnemius lateralis and m. biceps femoris were defined as the maximum of the smoothed EMG amplitude of these muscles during the ankle plantarflexion MVC and the knee flexion MVC respectively. The smoothed EMG signals of both muscles during both tasks and the recovery were normalized with respect to MVC. Finally, the average smoothed EMG amplitude during the recovery was subtracted from the smoothed EMG amplitude during tasks for both muscles (La Delfa et al., 2014). Smoothed baseline-subtracted EMG amplitude was averaged for each task over the full duration.

Statistical analysis

Mean metabolic power was statistically compared between: (1) the dynamic task and the isometric task, and (2) the initial rest and the recovery; both using two-tailed, paired sample *t*-tests. For both comparisons, the assumption of normality was tested using Kolmogorov–Smirnov tests (KS-tests) and effect sizes were determined using Cohen's *d*. Pilot studies had indicated that the difference in mean metabolic power between tasks was greater than the difference in mean metabolic power within one task between participants (i.e. Cohen's $d \geq 1$). The required sample size was determined with G*Power statistical software (Faul et al., 2007), using this estimated minimal effect size (Cohen's $d=1$), the chosen level of significance (alpha=0.05) and the desired statistical power (beta=0.95). Unless stated otherwise, results are expressed as mean± s.d., with s.d. referring to variation between participants. For one participant, gastrocnemius EMG data were discarded because signal-to-noise ratio was unacceptably low. For one other participant, all data were discarded because of a technical problem in the respirometry measurement. Statistical analysis was done on 15 participants for respirometry and motion capture data, and on 14 participants for gastrocnemius EMG data.

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RESULTS

Typical example

In Fig. 2, a typical example of the kinematics (panels i), kinetics (panels ii), mechanical power (panels iii) and antagonist muscle activation (panels vi) is shown for both the dynamic (A) and isometric (B) tasks. For this typical example, both left and right LL angle time-series closely resembled the target LL angle for both tasks. Consequently, both knee torque and knee joint mechanical power were close to the target knee torque and target knee joint mechanical power during both tasks. Knee torque could be ascribed almost exclusively to quadriceps force, because antagonistic muscle activation was low during both tasks.

Positive mechanical work, but not net mechanical work, differed between tasks

Average baseline-subtracted EMG amplitudes were below 1% MVC during both tasks (see Table 1), indicating that both antagonistic muscles were inactive. Frequency of LL angle oscillation during the dynamic task matched the target frequency of 0.54±0.01 Hz (mean±s.d.), because participants generally followed the target LL angle continuously (i.e. without skipping periods). Average LL angle during the isometric task was −0.39±0.03 rad for the left leg and −0.38±0.03 rad for the right leg, matching the target LL angle of −0.39±0.01 rad. Root-mean-squared error (RMSE) between the target LL angle and the LL angle time-series of each leg was low for both tasks (see Table 2). Moreover, movement was symmetrical, as RMSE between the LL angle time-series of each leg was low for both tasks (see Table 2). Because participants were able to correctly match both LL angles to the target, knee torque of both legs was close to the intended constant value during both tasks (Table 3). The dominant frequency of fluctuations in knee torque during the dynamic task was 1.50±0.21 Hz for both legs. Inspection of the knee torque power spectrum

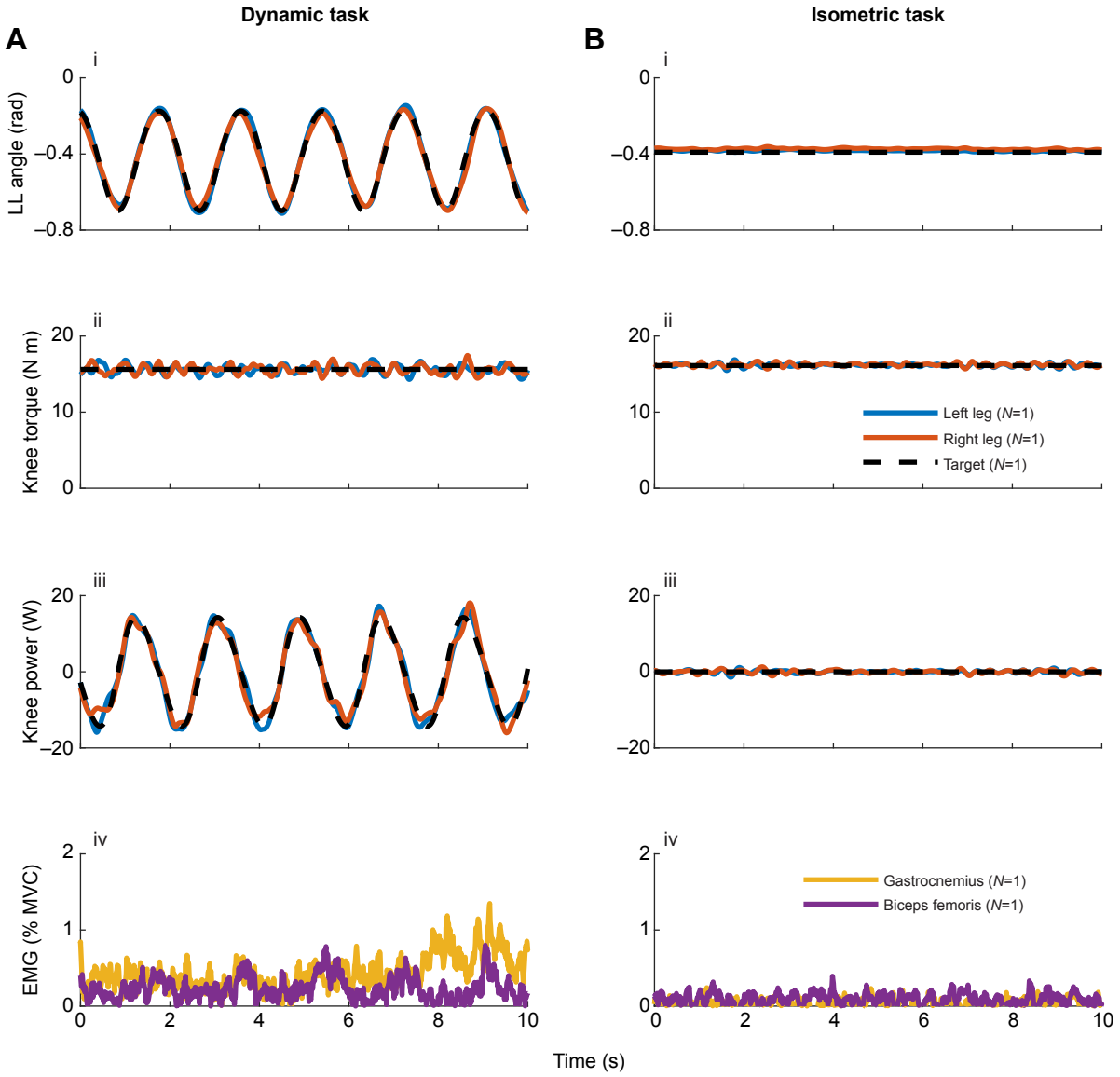

Fig. 2. Typical example of kinematics, kinetics and antagonistic muscle activation. Lower leg (LL) angle, knee torque, knee power and EMG in (A) the dynamic task and (B) the isometric task. (i) Target LL angle and LL angles of left and right leg during the dynamic task (Ai) and isometric task (Bi). (ii) Target knee torque and knee torque of left and right leg during the dynamic task (Aii) and isometric task (Bii). (iii) Target knee joint mechanical power and knee joint mechanical power of left and right leg during the dynamic task (Aiii) and isometric task (Biii). (iv) Smoothed baseline-subtracted EMG amplitude of gastrocnemius lateralis and biceps femoris during the dynamic task (Aiv) and isometric task (Biv). In all panels, *t*=0 s indicates 130 s after task initiation. For most panels, separate curves are difficult to distinguish because they are almost identical.

Table 1. Antagonistic muscle activation

	Mean EMG amplitude (% MVC)	
	Gastrocnemius lateralis	Biceps femoris
Dynamic task	0.44±0.58	0.50±0.64
Isometric task	0.51±0.98	0.35±0.74

Mean±s.d. baseline-subtracted EMG amplitude during both tasks as a percentage of EMG amplitude during maximal voluntary contraction (MVC) (*N*=14 for gastrocnemius lateralis and *N*=15 for biceps femoris).

revealed distinct peaks at the movement frequency and at its first two harmonics for most participants. Whereas this indicated a systematic effect of LL angle on knee joint torque during the dynamic task, knee joint torque RMSE was small compared with mean knee joint torque (Table 3). As expected, net knee joint mechanical work was zero for both tasks and for both legs. As intended, the within-cycle fluctuations in LL angle were substantial in the dynamic task and negligible in the isometric task. As a result, average positive knee joint mechanical power was substantially greater in the dynamic task compared with the isometric task (Table 3). Altogether, as intended, tasks differed in the amount of positive mechanical work done and were similar in terms of net mechanical work done, average knee torque and activation of antagonistic muscles.

Metabolic power reached steady-state and decayed exponentially for both tasks

In Fig. 3, time-series of $\dot{V}_{O_2}$, RER and metabolic power are shown. In each panel, two lines are shown; one indicating the mean of the participants that performed the dynamic task first and the other indicating the mean of the participants that performed the isometric task first. A plateauing of $\dot{V}_{O_2}$ and metabolic power occurred during both tasks (Fig. 3A and C, respectively). Both steady-state levels of $\dot{V}_{O_2}$ and metabolic power were substantially greater during the dynamic task than during the isometric task. A small increase of $\dot{V}_{O_2}$, RER and metabolic power occurred upon cessation of both tasks (Fig. 3). Subsequent decay of $\dot{V}_{O_2}$ occurred a few seconds after cessation of the dynamic task and about 10–15 s after cessation of the isometric task, returning to resting levels within 120 s.

Mean metabolic power was greater during the dynamic task than during the isometric task

The mean $\dot{V}_{O_2}$, RER and metabolic power during both resting periods (i.e. initial and recovery) and both tasks is shown in Table 4. The assumption of normality was met, as both differences in mean metabolic power between tasks and differences in mean metabolic power between resting periods could not be distinguished from a standard normal distribution (KS-tests yielded P=0.89 and P=0.58 respectively). For both periods of rest, mean metabolic power was similar (P=0.45, Cohen's d=0.21), indicating that participants fully recovered from the first task before performing the second task. Mean metabolic power was substantially and significantly greater for the dynamic task compared with the isometric task (P<0.0001, Cohen's d=4.2, mean±s.d. difference: 1.1±0.23 W kg^{-1}). Every participant had a greater mean metabolic power during the dynamic task than during the isometric task. Thus, as hypothesized, the dynamic task required more metabolic power than the isometric task.

Table 2. Kinematics

	RMSE of angle (rad)		
	Left leg–target	Right leg–target	Left leg–right leg
Dynamic task	0.06±0.02	0.06±0.02	0.03±0.01
Isometric task	0.00±0.00	0.00±0.00	0.01±0.00

Mean±s.d. RMSE between right leg, left leg and target lower leg angle (*N*=15).

DISCUSSION

Synopsis

The current study aimed at comparing the metabolic cost of doing alternating positive and negative muscle fibre mechanical work with the metabolic cost of doing zero muscle fibre mechanical work. This was accomplished by comparing mean metabolic power between an isometric and a dynamic task. To allow for an unbiased comparison, the experiment was set up such that net external mechanical work did not differ between tasks, and average joint torque was near-constant and marginally greater in the isometric task. In each participant, mean metabolic power was substantially smaller in the isometric task than in the dynamic task.

Validity of results

Muscle activation

Surface EMG amplitudes of antagonistic muscles acting around the knee were low (<1% MVC) and not substantially different between tasks. In contrast, the agonistic muscle (i.e. quadriceps) was required to provide a considerable amount of torque (~16 N m). Therefore, the quadriceps was the only substantially active muscle group, such that knee torque could be ascribed exclusively to quadriceps force in both tasks.

Kinematics and kinetics

All participants were able to match their lower leg angle to the target angle during both the isometric task and the dynamic task, resulting in an almost constant knee torque at the intended value, in both tasks. Whereas fluctuations in knee torque were somewhat greater during the dynamic task, these fluctuations were small compared with the mean knee torque. Controlling for knee torque is not equivalent to controlling for quadriceps force, because the moment arm of m. quadriceps femoris about the knee is dependent on knee angle. However, for the range of knee angles used in the present experiment, variation in moment arm is small (Krevolin et al., 2004). Therefore, controlling for average knee joint torque was near-equivalent to controlling for average total quadriceps force. Near-constant quadriceps force implied near-constant quadriceps tendon length. Thus, the variation in muscle–tendon complex length due to joint angular change during the dynamic task was almost entirely taken up by the muscle fibres. The dynamic task thereby consisted of alternating muscle fibre shortening and lengthening, whereas the isometric task consisted of near-isometric muscle fibre contraction, at an equivalent average total quadriceps force and net mechanical work.

Respirometry

Close inspection of Fig. 3 reveals that, even though $\dot{V}_{O_2}$ plateaued towards the end of each task, $\dot{V}_{O_2}$ and RER increased immediately after cessation of both tasks. The increase in RER suggests that blood flow occlusion may have occurred. Blood flow occlusion has previously been observed for tasks with low muscle fibre contraction velocity in combination with constant muscle force (Sjøgaard et al., 1988). Considering that the steady state $\dot{V}_{O_2}$ was substantially lower in the isometric task compared with the dynamic task, the observation that the relaxation of $\dot{V}_{O_2}$ and RER during recovery was similar for both tasks suggests that blood flow occlusion was more prominent during the isometric task. Information on the oxygen debt resulting

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Table 3. Kinetics

	Average knee torque (N m)			RMSE of knee torque (N m)			Average positive power (W)		
	Left leg	Right leg	Target	Left leg	Right leg	Target	Left leg	Right leg	Target
Dynamic task	15.2±1.8	15.2±1.7	15.2±1.8	0.9±0.1	0.9±0.1	0	4.3±0.6	4.3±0.5	4.2±0.4
Isometric task	15.7±1.7	15.7±1.7	15.7±1.8	0.2±0.1	0.2±0.1	0	0.1±0.1	0.1±0.1	0

Mean±s.d. average knee torque, RMSE of knee torque and average positive knee joint mechanical power of target, left leg and right leg for both tasks (N=15).

from blood flow occlusion can be obtained by considering recovery metabolism. Given our protocol (Fig. 1B), recovery metabolism was only measured after the first task performed by any participant. As the order of tasks was counterbalanced, this implies that recovery respirometry data for both the isometric and the dynamic task were available for half of the participants. The between-tasks difference in metabolic energy consumed during the first task performed by each participant was 268.0 J kg^{-1}. This value is much greater than the

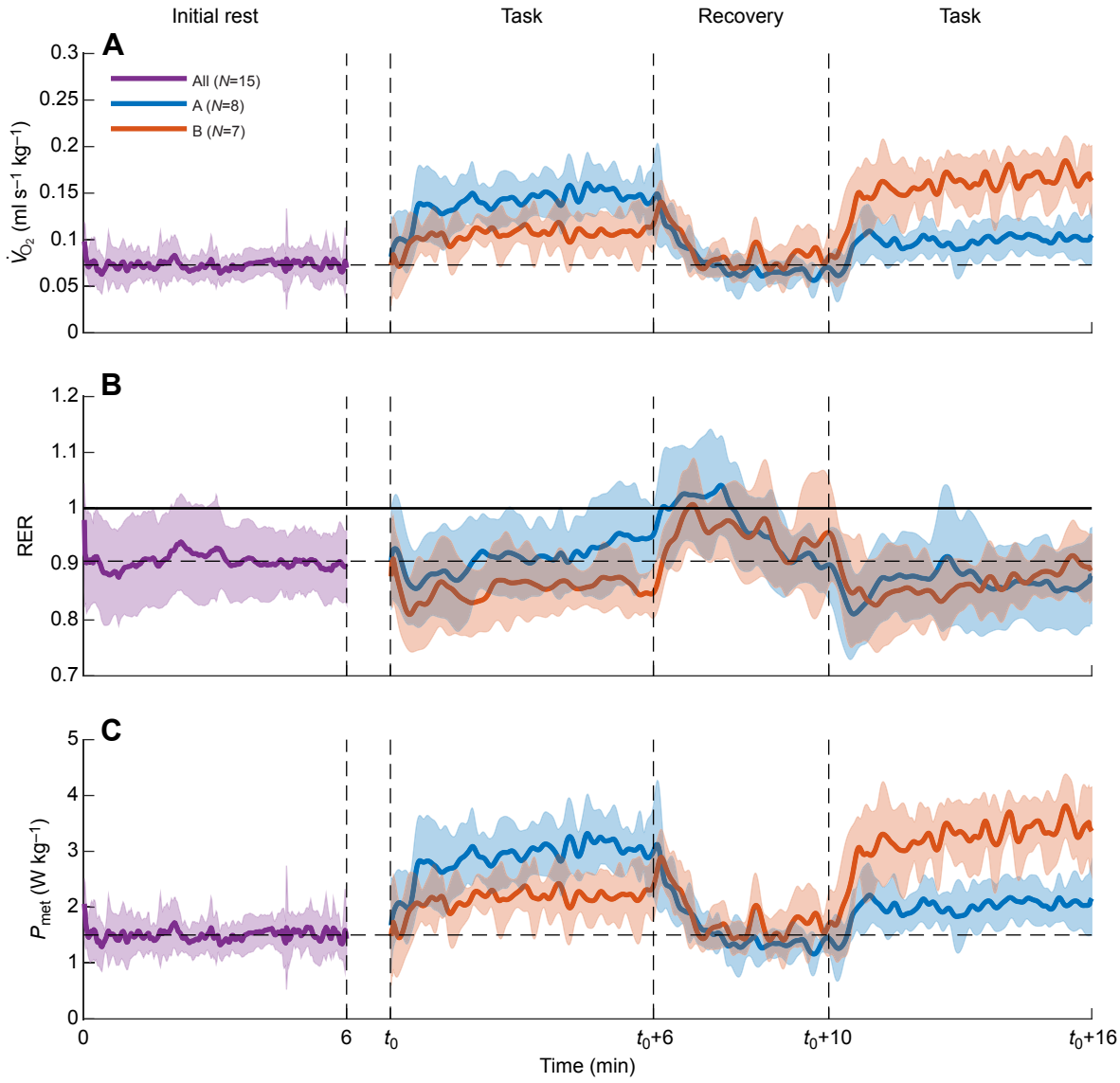

Fig. 3. Respirometry time-series. Time-series of respirometry measurements during the experiment, shown as mean across participants (solid lines) as well as mean±1 s.d. across participants (shaded areas). Respirometry time-series during the initial rest measurement (purple) were used to obtain the resting time-average (horizontal dashed black lines). In chronological order, the experiment consisted of the initial rest, the first task, the recovery and the second task (each part delineated by vertical dashed black lines). One group of participants (group A, N=8) performed the dynamic task first and the isometric task second (shown in blue). Another group of participants (group B, N=7) performed the isometric task first and the dynamic task second (shown in red). (A) Rate of oxygen uptake ($\dot{V}_{O_2}$), showing steady state during tasks and small increase after cessation. (B) Respiratory exchange ratio (RER), showing steady-state during tasks and small increase after cessation. The solid black line shows RER=1, i.e. values below this line reflect aerobic metabolism. (C) Gross metabolic power (P_{met}), showing steady-state during tasks and small increase after cessation. A two-tailed, paired sample t-test indicated that P_{met} was greater during the dynamic task than during the isometric task (P<0.0001) and not different between the initial rest and the recovery (P=0.45). A small increase directly after exercise cessation indicates some anaerobic metabolism occurring during the tasks, possibly due to blood flow occlusion. All data are summarized in Table 4.

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Table 4. Respirometry and metabolic power measurements

	$\dot{V}_{O_2}$ (ml s^{-1} kg^{-1})	RER	P_{met} (W kg^{-1})
Initial rest	0.073±0.012	0.90±0.05	1.51±0.23
Recovery	0.072±0.012	0.94±0.06	1.49±0.24
Dynamic task	0.156±0.022	0.90±0.06	3.22±0.46
Isometric task	0.104±0.017	0.86±0.06	2.13±0.36

Mean±s.d. $\dot{V}_{O_2}$, respiratory exchange ratio (RER) and gross metabolic power (P_{met}) during both rest periods and both tasks (N=15).

difference in metabolic energy consumed during the subsequent recovery period, which was 47.6 J kg^{-1}. Moreover, the significance of the latter difference is questionable, as the standard deviations between participants within each group were similar to the mean difference between these groups (s.d. for recovery after dynamic task: 44.2 J kg^{-1} and s.d. for recovery after isometric task: 39.5 J kg^{-1}). Thus, blood flow occlusion cannot explain the large difference in metabolic power between the isometric and dynamic task.

Metabolic cost per unit force during the isometric task

The net metabolic power per unit force in the isometric task was 0.058 W N^{-1}, which is substantially more than the 0.020 W N^{-1} reported by Ortega et al. (2015). This discrepancy likely reflects an overestimation of metabolic cost associated with isometric contraction in the current study, together with an underestimation of metabolic cost associated with isometric contraction in Ortega et al. (2015). Although we expect that the majority of baseline-subtracted metabolic power was caused by quadriceps muscle force production, a small part of it may have been due to an increased level of contraction of other muscles (e.g. respiratory muscles, heart) and elevated metabolism in organs (e.g. lungs, liver, brain). In contrast, Ortega et al. (2015) determined metabolic cost at the muscle-level using phosphorus magnetic resonance spectrometry. This technique is likely to slightly underestimate of metabolic cost, because glycolytic adenosine triphosphate synthesis is neglected (Blei et al., 1993). Considering the smaller values reported in Ortega et al. (2015), it is unlikely that the metabolic power per unit force in the isometric task was underestimated in the present study.

Mechanical efficiency during the dynamic task

Baseline-subtracted mechanical efficiency of doing positive mechanical work was in the order of 9% during the dynamic task. To calculate this value, it was assumed that positive mechanical power requires 3.6 times more metabolic power than negative mechanical power (Abbott et al., 1952). To determine if this value for mechanical efficiency of doing positive work is reasonable, muscle contraction velocity must be considered, because mechanical efficiency depends on shortening velocity (Fenn, 1924; Hill, 1938; Barclay et al., 1993). Knee joint angular velocity was 0.6 rad s^{-1} on average during the extension phase of the dynamic task. Using parameter values for muscle fibre optimum length ($l_{CE,opt}$) and muscle moment arms as reported in van Soest et al. (1993), muscle fibre contraction velocity during the dynamic task was estimated to be 0.025 m s^{-1}, which corresponds to 0.3 $l_{CE,opt}$ s^{-1}. The latter value is about 2.5% of maximal shortening velocity (de Ruiter et al., 2000), which is much slower than the relative shortening velocity at which mechanical efficiency is maximal (e.g. Barclay et al., 1993). Considering (1) that mechanical efficiency of doing positive work in intact humans has never been reported to exceed 25% [as reported by Margaria (1968) for uphill walking], and (2) that mechanical efficiency decreases sharply when muscle fibre contraction velocity approaches zero (Barclay et al., 1993), the estimated mechanical efficiency of doing positive work during the dynamic task in this study is in line with the literature.

Explanation of results

Task order was balanced across participants, meaning that time-dependent processes such as accumulating muscle fatigue cannot explain the differences between tasks. In addition, the observed difference in metabolic cost per unit force between tasks cannot be due to a difference in average muscle force, because muscle force was similar between tasks. Similarly, the observed difference in metabolic cost per unit force between tasks cannot be due to a difference in net mechanical work done, because net mechanical work was negligible in both tasks. The isometric task and the dynamic task differed in the amount of positive and negative muscle fibre mechanical work done, which were negligible in the former and substantial in the latter. Of these two work terms, positive muscle fibre mechanical work is more likely than negative muscle fibre mechanical work to have caused the difference in metabolic cost per unit force (e.g. Abbott et al., 1952). Altogether, the most plausible explanation for the difference in metabolic cost per unit force is the difference in positive muscle fibre mechanical work. Yet, there are alternative explanations to be considered.

Possible alternative explanations

Difference in active muscle fibre type between tasks

Fast twitch muscle fibres consume more metabolic energy per unit force than slow twitch muscle fibres (Crow and Kushmerick, 1982). Therefore, an alternative explanation for why the dynamic task required more metabolic energy than the isometric task is that a greater percentage of fast twitch muscle fibres was active. However, at low relative force/activation level (Henneman et al., 1965), low contraction velocity (Kaya et al., 2008) and large task duration (Sargeant and de Haan, 2006) slow twitch muscle fibres are primarily recruited. These conditions apply to both tasks, because relative force was small, contraction velocity was about 2.5% of maximal shortening velocity and task duration was 360 s. Therefore, we expect that slow twitch muscle fibres were primarily recruited in both tasks; any difference in active muscle fibre type between tasks cannot explain the key results of this study.

Muscle history effects

Recent *in vitro* studies have indicated that muscle history effects may reduce the metabolic cost of muscle fibre contractions (Joumaa and Herzog, 2013; Joumaa et al., 2017). Residual force enhancement in skinned fibres has been reported to decrease metabolic cost of isometric force production by 17.2±4.1% (mean± s.d.) over a period of 40 s (Joumaa and Herzog, 2013). Reduction of metabolic cost was largest at fibre lengths that exceed optimum length. In contrast, force depression does not affect the metabolic cost of isometric force production (Joumaa et al., 2017). It is unclear to what extent these results can be generalized to prolonged *in vivo* contractions at fibre lengths below optimum length. It is unclear whether muscle history effects were present during the dynamic task because EMG was not measured in the knee extensor muscles. Therefore, it is impossible to know which parts of the quadriceps muscle were active during lengthening and which parts were active during shortening. If different parts of the quadriceps muscle were active during lengthening than during shortening, no muscle history effects would have been present. However, this is unlikely to have occurred when considering the load sharing principle (e.g. Seireg and Arvikar, 1975). Even if muscle history effects were present, the

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effect on metabolic cost must have been small in comparison to differences in metabolic cost observed in this study. Therefore, history effects at best explain a small part of the key results of this study.

Fluctuations in muscle activation during the dynamic task

Owing to the force–velocity relationship and to the observation that knee torque was constant, we expect quadriceps muscle activation to be greater during shortening than during lengthening. In addition to the force–velocity relationship, we expect fluctuations in muscle activation due to the force–length relationship. Taking the moment arm of the quadriceps to be about 0.04 m, knee angle change in the dynamic task (0.52–1.05 rad away from full extension) corresponds to a 0.021 m change in fibre length. Using the previously mentioned parameter value for $l_{CE,opt}$ as reported in van Soest et al. (1993), muscle fibre length change was estimated to be 0.23 $l_{CE,opt}$ during the dynamic task. Thus, the position of quadriceps muscle fibres on their force–length relationship changed substantially during the dynamic task. In contrast, quadriceps muscle fibre length did not change during the isometric task. Because the plateau of the quadriceps torque-angle relationship is commonly reported to be at about 1.05–1.40 rad away from full extension (Marginson and Eston, 2001), both tasks were performed on the ascending limb of the force–length relationship. We estimate the maximum isometric force at the most extended position occurring in the dynamic task to be 55% of the maximum isometric force at the most flexed position (Ichinose et al., 1997; Marginson and Eston, 2001). Therefore, due to the force–length relationship, participants must have increased activation level near extension in order to maintain the desired knee extension torque. Activating and deactivating a muscle requires metabolic energy, regardless of the total stimulation time (Hogan et al., 1998) and the total amount of positive mechanical work done (Doke and Kuo, 2007). Therefore, such fluctuations in muscle activation may explain part of the greater mean metabolic power during the dynamic task compared with the isometric task.

Explanation of results after considering alternatives

Based on the above discussion, we conclude that the alternative explanations together cannot explain the large difference in metabolic cost between tasks. Overall, our explanation is that the substantially greater metabolic cost in the dynamic task is largely due to the positive muscle fibre mechanical work done, and to some extent due to fluctuations in muscle activation.

Conclusions

At essentially identical average muscle force and identical net external mechanical work in an *in vivo* experiment, mean metabolic power was substantially greater in a dynamic task compared to an isometric task. Because positive muscle fibre mechanical work was negligible during the isometric task and substantial during the dynamic task, this suggests that the metabolic cost of near-constant muscle force production *in vivo* at zero net mechanical work can be reduced by minimizing positive muscle fibre mechanical work.

APPENDIX

In this appendix, we explain why periodic knee flexion–extension movements in the vertical plane exist at which knee torque is constant, and explain how we calculated the movements that participants were asked to track.

We modelled shank, foot and lead strap as a single rigid body referred to as LL, and we considered the pendulum-like motion of LL in the vertical plane, driven by the knee torque (T_{knee}). Pendulum orientation and angular acceleration were described by ϕ_{LL} and α_{LL}, respectively (see Fig. A1). LL mass (m_{LL}), centre of mass location with respect to the knee ($d_{LL/knee}$) and moment of inertia with respect to the knee ($J_{LL/knee}$) were determined by the participant's inertial parameters (see Materials and Methods). The dynamics of this 1-DOF system was most conveniently described in terms of the rotational equation of motion, taking the knee axis that is assumed not to move as the pivot point:

$$J_{LL/knee} \cdot \alpha_{LL} - T_G = T_{knee}, \quad \text{(A1)}$$

where T_G is the torque due to the force of gravity. Thus (taking $g<0$):

$$J_{LL/knee} \cdot \alpha_{LL} - m_{LL} \cdot g \cdot d_{LL/knee} \cdot \cos(\phi_{LL}(t)) = T_{knee}. \quad \text{(A2)}$$

From Eqn A2, the equilibrium condition is immediately clear:

$$T_{knee,eq} + m_{LL} \cdot g \cdot d_{LL/knee} \cdot \cos(\phi_{LL,eq}) = 0. \quad \text{(A3)}$$

Note that the gravitational torque depends on ϕ_{LL}, and thus constitutes a spring-like term. Further note that whenever the vertical coordinate of the centre of mass is negative (see Fig. A1), the corresponding linearized gravitational stiffness [i.e. $m_{LL} \cdot \boldsymbol{g} \cdot d_{LL/knee} \cdot \sin(\phi_{LL})$] is positive. This implies that (1) for any equilibrium position $\phi_{LL,eq}$, the corresponding $T_{knee,eq}$ can be found from Eqn A3, and (2) that upon perturbation from this equilibrium position, for this time-invariant $T_{knee,eq}$, a periodic motion will occur that is defined by Eqn A2.

Based on pilot experiments, we predefined the extreme values of ϕ_{LL} in the range between 0 and $-\pi/2$ (see main text). We then determined the constant value of T_{knee} that was consistent with a periodic motion between the extreme ϕ_{LL} values chosen, for each participant individually. Finally, note that the oscillation frequency

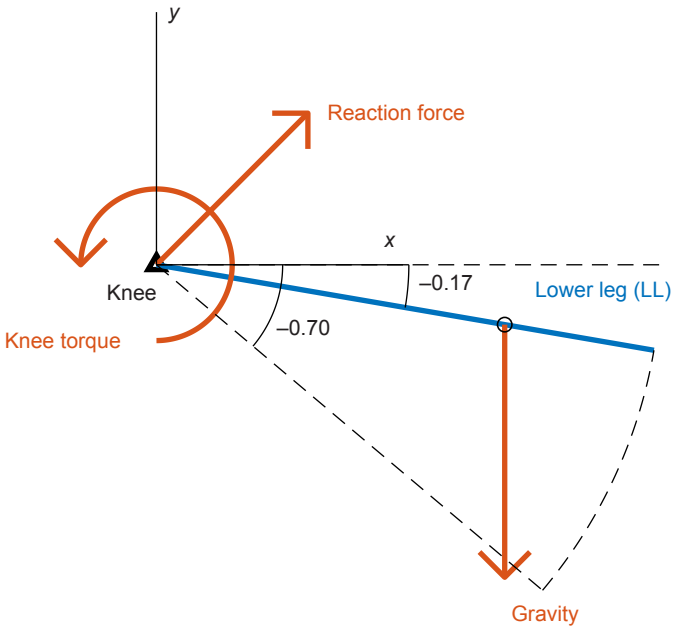

Figure A1. Free-body diagram of the lower leg segment. Shank, foot and lead strap together form the lower leg segment, which is modelled as a single rigid body referred to as LL. The sum of knee torque and the torque exerted by gravity can cause a pendulum-like motion of LL in the vertical plane between –0.17 rad and –0.70 rad ('dynamic task'). Alternatively, knee torque and gravitational torque could sum to zero, such that static equilibrium is reached ('isometric task').

of the resulting motion cannot be chosen freely; rather, it follows from the inertial properties and the range of LL angles visited.

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Competing interests
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